MARINE MAMMAL SCIENCE, 14(3):460–489 (July 1998)
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SEASONAL PATTERNS IN THE ABUNDANCE AND DISTRIBUTION OF CALIFORNIA CETACEANS, 1991–1992

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ABSTRACT

This study presents a detailed seasonal comparison of the abundance and distribution of cetaceans within 100–150 nmi (185–278 km) of the California coast during 1991 and 1992. The results of a shipboard line-transect survey conducted in July–November 1991 ("summer") were compared to those from aerial line-transect surveys conducted in March–April 1991 and February–April 1992 ("winter"). Using a confidence-interval-based bootstrap procedure, abundance estimates for six of the eleven species included in the comparison exhibited significant ($\alpha = 0.05$) differences between the winter and summer surveys. Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), Risso's dolphins (*Grampus griseus*), common dolphins (*Delphinus* spp.), and northern right whale dolphins (*Lissodelphis borealis*) were significantly more abundant in winter. The abundance of blue whales (*Balaenoptera musculus*) and gray whales (*Eschrichtius robustus*) reflected well-documented migratory patterns. Fin whales (*B. physalus*) were significantly more abundant during summer. No significant differences in seasonal abundance were identified for Dall's porpoises (*Phocoenoides dalli*), bottlenose dolphins (*Tursiops truncatus*), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), or humpback whales (*Megaptera novaeangliae*). Significant north/south shifts in distribution were found for Dall's porpoises, common dolphins, and Pacific white-sided dolphins, and significant inshore/offshore differences were identified for northern right whale dolphins and humpback whales.

Key words: California, North Pacific, cetacean, whale, dolphin, porpoise, line transect, aerial survey, ship survey, abundance, distribution, seasonality, bootstrap, confidence-interval test.

Coastal waters of the California Current support a rich and diverse marine fauna, including at least 30 species of cetaceans (Leatherwood *et al.* 1982*a*). This eastern boundary current represents a mixing ground for four different

water masses: subarctic waters from the north, tropical waters from the south, warm, oligotrophic waters from the west, and cool, nutrient-rich waters that upwell from below (Reid *et al.* 1958). Pronounced seasonal, interannual, and decadal scale variability in oceanographic conditions and biological productivity has been documented (Reid *et al.* 1958, Pavlova 1966, Chelton *et al.* 1982, Roemmich and McGowan 1995). It has also long been known that the abundance of some cetacean species changes on both seasonal and interannual time scales (Norris and Prescott 1961, Leatherwood and Walker 1979), but these patterns have not previously been documented quantitatively. In 1975–1978 and 1980–1983, year-round aerial surveys were conducted in southern and north-central California, respectively, to investigate seasonal patterns in cetacean distribution and abundance (Dohl *et al.* 1980, 1983, 1986). Although the results of these studies suggested some seasonal variability in the abundance of some species, no statistically based comparisons were made.

In 1991 and 1992, two complementary line-transect surveys covering cold-water and warm-water periods were conducted along the California coast to estimate the abundance of cetaceans. An aerial survey was conducted within 100–150 nmi (185–278 km) of the California coast during the cold-water periods (February–April) of 1991 and 1992, and a shipboard survey extending 300 nmi (556 km) offshore was conducted during the warm-water months (July–November) of 1991. Abundance estimates from these two surveys have been published in separate papers (Barlow 1995, Forney *et al.* 1995). A direct seasonal comparison was not made in these earlier publications because the shipboard survey covered a larger area than the aerial survey. However, it is useful to examine and quantitatively document seasonal changes in abundance and distribution to further our understanding of cetacean ecology and to provide a better basis for the management of these species. In this paper we present a line-transect analysis for the subset of the shipboard survey data which falls within the aerial survey study area and compare statistically the resulting abundance estimates with the previously published aerial survey estimates using a bootstrap technique. For species with sufficient sightings in both seasons, a similar bootstrap test is used to investigate seasonal differences in distribution for north/south and inshore/offshore strata. The observed seasonal patterns in abundance and distribution within this region in 1991–1992 are discussed on a species-specific basis, along with known caveats and biases in the methods used for the two different types of surveys. For simplicity, the aerial and shipboard surveys will be referred to as "winter" and "summer" surveys, respectively; however, it is important to bear in mind that the survey platforms differed for the two seasons and that the described patterns of distribution and abundance in 1991–1992 may differ from seasonal patterns in other years.

METHODS

Aerial Survey Methods, Winter 1991 and 1992

Detailed descriptions of the aerial survey field methods and analytical procedures have been previously published (Carretta and Forney 1993, Forney *et*
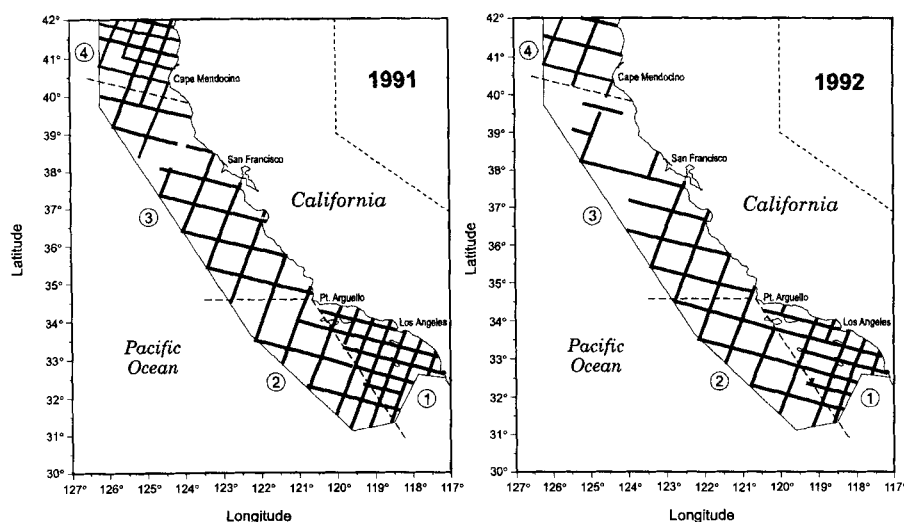
Figure 1.   Completed transects (thick lines) for aerial line-transect survey conducted off California in February–March 1991 and February–April 1992. Thin line denotes study area boundary, extending 100 nmi (185 km) offshore in central and northern California, and approximately 150 nmi (278 km) offshore in southern California. Circled numbers refer to areas used for stratification, with stratum boundaries marked by dashed lines.

al. 1995), and only the most important aspects of the methods will be summarized here. In March–April of 1991 and February–April of 1992, a twin-engine, turbo-prop Twin Otter aircraft was used to survey along two predetermined sets of overlapping transect grids. The grids were designed to cover waters systematically along the entire California coastline out to 100 nmi (185 km) off central and northern California and to 150 nmi (278 km) off southern California, corresponding to approximately 3,000–4,000 m water depth. Although poor weather prevented the completion of all transect lines, coverage was comparable in the two years and extended along the entire California coast (Fig. 1). The aircraft flew at approximately 213 m (700 ft) altitude and an airspeed of 185 km h^{-1} (100 kn), in sea state conditions of 0–4 on the Beaufort scale.

All cetacean sightings were recorded following line-transect methodology (Burnham *et al.* 1980, Buckland *et al.* 1993*a*). Perpendicular distances were calculated from the aircraft's altitude and the declination angle to the sighting (obtained with a hand-held clinometer, where 90° is directly below the aircraft and 0° is at the horizon). Upon sighting cetaceans, search effort was suspended and the aircraft circled over the animals until species identification and group-size estimates had been obtained, or until visual contact with the animals was lost. Species were identified by mutual agreement of all observers who were able to obtain an adequate view of the animals, and group-size estimates were made separately and confidentially by each observer. A conditionally independent design involving a primary and secondary observer team (Barlow 1995,

Forney *et al.* 1995) allowed the estimation of the fraction of animals missed on the trackline due to perception bias (Marsh and Sinclair 1989). The two primary observers viewed downward and laterally through bubble windows on each side of the aircraft, and the secondary observer searched below the aircraft through a "belly" window but waited to report sightings until they had been missed by the primary team.

The previously published abundance estimates (Forney *et al.* 1995) are used in the present analysis without any changes. In that analysis the data were stratified by area (see Fig. 1), group-size categories, and species groups (Forney *et al.* 1995). Geographic strata were chosen on the basis of oceanographic boundaries and survey coverage. Because sample sizes were small for most cetaceans seen, species with similar school size, body size, and behavior were initially combined subjectively and then evaluated on the basis of their perpendicular sighting distributions. Species groupings and group-size strata with distributions that did not differ statistically (Kolmogorov-Smirnov test) were further combined while trying to equalize sample sizes as much as possible (Table 1). [Although an objective statistical measure, such as Akaike's Information Criterion (AIC; Akaike 1973) is usually preferable for determining strata, the method used in Forney *et al.* (1995) effectively evaluated similar criteria, and it is not expected that the strata would have been significantly different if AIC had been used.] Abundances were estimated according to standard line-transect methods (Burnham *et al.* 1980, Buckland *et al.* 1993*a*) using the equation:

$$N_k = \sum_{i=1}^{4} \sum_{j=1}^{3} \frac{A_i n_{i,j,k} s_{i,j,k} f_{j,k}(0)}{2 L_i g_{j,k}(0)} \tag{1}$$

where

N_k = estimated total number of animals of species k in the study area,

$n_{i,j,k}$ = number of sightings of groups of species k in Area i with school sizes falling into group-size category j,

$s_{i,j,k}$ = average group size for groups of species k in Area i and group-size category j, calculated as the total number of animals in all groups divided by the number of groups sighted,

$f_{j,k}(0)$ = the probability density function evaluated at zero perpendicular distance for group-size category j of the species group to which species k belongs (in km^{-1}),

$g_{j,k}(0)$ = the probability of detecting a group of animals on the transect line for group-size category j of the species group to which species k belongs,

L_i = the length of transect surveyed in Area i (in km), and

A_i = the size of Area i (in km^2).

Values for $f(0)$ were obtained for each species/group-size category by fitting the distribution of perpendicular sighting distances (for all areas combined,

Table 1. Species groups and parameters used for abundance estimation from aerial survey data for species included in this seasonal comparison. See Equation 1 for definitions of variables. Subscripts correspond to area strata in Figure 1. Asterisks (*) indicate species for which an approximate correction for availability bias was made (see Methods and Discussion sections).

Small cetaceans	Group size	$f(0)$	$g(0)$	n_1	s_1	n_2	s_2	n_3	s_3	n_4	s_4
Dall's porpoise, *Phocoenoides dalli*	1–10	4.70	0.22*	9	4.00	2	4.50	19	2.63	8	3.00
Pacific white-sided dolphin,	1–10	4.70	0.67	1	4.00	2	5.50	1	1.00	0	—
Lagenorhynchus obliquidens	>10	2.85	0.85	4	29.75	5	95.00	6	276.50	2	457
Risso's dolphin,	1–10	4.70	0.67	6	7.83	1	8.00	0	—	0	—
Grampus griseus	>10	2.85	0.85	8	44.00	0	—	4	124.25	0	—
Bottlenose dolphin,	1–10	4.70	0.67	1	9.00	0	—	1	1.00	0	—
Tursiops truncatus	>10	2.85	0.85	6	22.17	0	—	0	—	0	—
Common dolphins,	1–10	4.70	0.67	3	8.00	0	—	0	—	0	—
Delphinus delphis and *D. capensis*	>10	2.85	0.85	19	685.05	4	176.00	1	157.00	0	—
Northern right whale dolphin,	1–10	4.70	0.67	13	5.85	1	9.00	3	6.00	1	2.00
Lissodelphis borealis	>10	2.85	0.85	5	29.20	3	72.33	3	17.67	2	33.00
Medium and large cetaceans (All group sizes)		$f(0)$	$g(0)$	n_1	s_1	n_2	s_2	n_3	s_3	n_4	s_4
Killer whale, *Orcinus orca*		2.49	0.95	0	—	1	1.00	0	—	1	1.00
Sperm whale, *Physeter macrocephalus*		2.49	0.32*	0	—	2	14.50	1	1.00	0	—
Gray whale, *Eschrichtius robustus*		2.49	0.95	12	3.42	0	—	11	5.27	2	3.00
Humpback whale, *Megaptera novaeangliae*		2.49	0.95	1	1.00	0	—	2	1.50	5	1.80
Blue whale, *B. musculus*		2.49	0.95	0	—	1	1.00	0	—	0	—
Fin whale, *B. physalus*		2.49	0.95	2	1.50	0	—	0	—	0	—

Area sizes: $A_1 = 46{,}300$ km² $\quad A_2 = 63{,}772$ km² $\quad A_3 = 120{,}108$ km² $\quad A_4 = 34{,}090$ km²

Length of transect surveyed: $L_1 = 3{,}715$ km $\quad L_2 = 2{,}831$ km $\quad L_3 = 4{,}461$ km $\quad L = 2{,}035$ km

primary and secondary sightings, distances measured in km) to the Hazard rate model with the program HAZARD (Buckland 1985). The resulting detection function, $g(x)$, describes the probability of sighting a group of animals at distance x. The probability density function, $f(x)$, is then calculated as $f(x) = g(x)/\int g(x)\ dx$, and $f(0) = 1/\int g(x)\ dx$, assuming $g(0) = 1$ (Buckland *et al.* 1993*a*). Because $g(0) < 1$ for aerial surveys of cetaceans, $g(0)$ was estimated following the methods described in Forney and Barlow (1993). Due to small sample sizes, it was not possible to estimate the variance in $g(0)$. This should result in a downward bias in the variance of the abundance estimates, but bias in the abundance estimates themselves will be reduced. When published data were available, an estimate of availability bias (Marsh and Sinclair 1989), *i.e.*, the fraction of animals missed because they are submerged at the time the aircraft passes overhead, was included in the calculation of $g(0)$. However, for most species no such correction factors were available. This important source of bias will be addressed in more detail in the Discussion section when evaluating the results of this analysis. The lengths of transect lines flown, L_i, and total area sizes, A_i, are given in Table 1.

Variances were estimated using a bootstrap procedure in which random segments of 50 km length from the actual survey data were subsampled with replacement to simulate 1,000 equivalent surveys. For each simulated survey, sightings were first stratified into the three species/group-size categories (Table 1), and individual values for n and s were calculated. The parameter $f(0)$ was re-estimated for each simulated data set with the program HAZARD. Because small sample sizes presented a problem in re-estimating $g(0)$ for each bootstrap replicate, the value estimated for the actual data was used and treated as a constant known without error. Following these procedures, 1000 bootstrap abundance estimates (N^*) were obtained for all species, and variances and coefficients of variation (CV) were calculated from these 1,000 values of N^* using standard formulae.

Ship Survey Methods, Summer 1991

The field methods for the ship surveys are described in detail in Barlow (1995). The survey platform was the 52-m NOAA research vessel *McArthur*, which covered a systematic grid of transect lines out to 300 nmi (556 km) from the California coast between 27 July and 6 November 1991 (Fig. 2). Teams of three observers searched during 2-h watches, rotating between port observer, starboard observer, and data recorder positions. The data recorder was responsible for entering all environmental and sighting information into a laptop computer, as well as monitoring the region in front of the vessel and near the transect line for animals using naked eye and 7X binoculars. The two other observers searched for animals with 25X binoculars. Upon sighting cetaceans, the vessel was generally diverted for species identification and group-size estimation. Species identification was agreed upon by the team of observers, which at all times included at least one identification specialist. All observers estimated species composition (for multispecies groups) and recorded
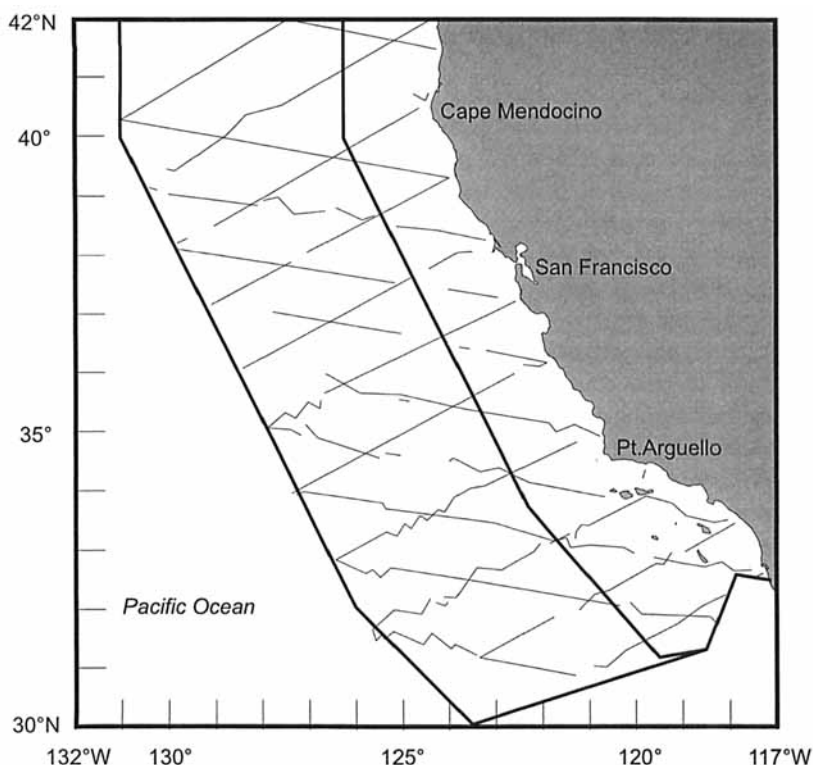
Figure 2. Completed transects (thin lines) for shipboard line-transect survey con-
ducted off California in July–November 1991. Outer thick line is boundary of entire
study area for that survey; inner thick line is boundary of smaller aerial survey study
area used in present analysis.

best, maximum, and minimum group-size estimates separately and confiden-
tially to avoid influencing one another. The mean value of all observers' best
estimates was used in the analysis. Previous studies involving calibration
counts from aerial photographs of dolphin schools have shown this to be a
good estimator of the true group size (Gerrodette and Perrin 1991).

In the analysis presented below, cetacean abundances were re-estimated for
the smaller aerial survey study area (Fig. 2) using the same methodology as
Barlow (1995). AIC (Akaike 1973) was used to objectively determine the best
stratification regime for estimating $f(0)$, using the Hazard rate model. Strat-
ifications considered were sea-state conditions (calm: Beaufort sea states 0–2;
rough: Beaufort sea states 3–5), species or species groups, group sizes, and the
four geographic strata used in the aerial survey analysis. Preliminary species
groupings and group-size categories were created on the basis of similarities
in body size, group size, and behavior. An iterative approach was then applied
to test other species combinations and group-size ranges and determine the
stratification that minimized AIC. The resulting strata were qualitatively sim-
ilar to those obtained by Barlow (1995), although small and large delphinids

were combined because of small sample sizes, and the group-size categories differed for this new "small cetacean" group (Table 2). Additionally, small whales were excluded from this analysis because too few sightings were made to estimate the perpendicular distance distribution function. The distributions of perpendicular sighting distances and Hazard model fits are shown in Figure 3. Abundance estimates for all cetacean species were calculated as:

$$N_k = \sum_{j=1}^{3} \frac{A\, n_{j,k}\, s_{j,k}\, f_{j,k}(0)}{2\, L\, g_{j,k}(0)} \tag{2}$$

where

N_k = estimated total number of animals of species k in the study area,

$n_{j,k}$ = number of sightings of species k in group-size category j,

$s_{j,k}$ = average group size of species k in group-size category j,

$f_{j,k}(0)$ = the probability density function evaluated at zero perpendicular distance for group-size category j of the species group to which species k belongs (in km^{-1}),

$g_{j,k}(0)$ = the probability of detecting a group of animals on the transect line for group-size category j of the species group to which species k belongs,

L = the length of transect surveyed (in km), and

A = the size of the study area (in km^2).

The fraction of groups seen, $g(0)$, was estimated according to the formulae provided in the appendix of Barlow (1995). Variances in abundance estimates were also obtained as in Barlow (1995), using a bootstrap method in which the survey was divided into segments of equal length and then these segments subsampled with replacement to simulate 1,000 surveys. Barlow used segments of 75 nmi (139 km) length (corresponding roughly to one day's survey effort), but because of the reduced width of the study area for this comparison, 50-nmi (93-km) segments were used in the present analysis. Previous studies have shown that a broad range of segment lengths results in similar estimates of variance (Forney and Barlow 1993, Barlow 1993). For each simulated survey, abundance estimates (N^*) were computed, and variances and coefficients of variation were calculated from these 1,000 estimates using standard formulae.

Statistical Comparisons of Estimates

For normally distributed populations, two means with estimates of variance can easily be compared using a standard t or z test (Zar 1984). However, estimates of animal abundance often have positively skewed distributions (Buckland *et al.* 1993a), rendering these standard tests inappropriate. Alternately, tests based on confidence intervals can be used to compare the means
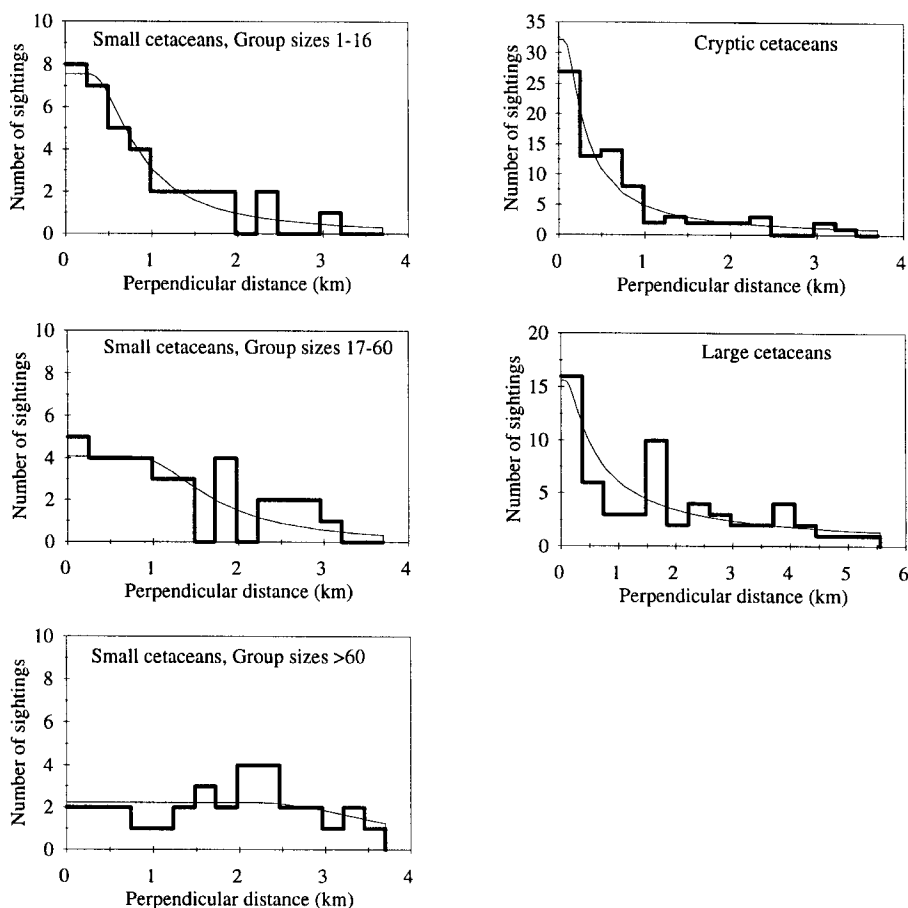
Table 2. Species groups and parameters for abundance estimates from ship survey data (see Equation 2 for definitions of variables; subscripts refer to indicated group-size strata). Values of $f(0)$ in units of km^{-1}. [Note: species-specific mean group sizes may be smaller than group-size range for particular stratum, because some species are commonly seen in small subgroups within a large multispecies group.]

Cryptic cetaceans (Truncated at 3.70 km; sea states 0–2)

	n_1	s_1	$f(0)_1$	$g(0)_1$
Dall's porpoise, *Phocoenoides dalli*	50	3.13	1.627	0.768

Small cetaceans (Truncated at 3.70 km; sea states 0–5)

	Group sizes 1–16				Group sizes 17–60				Group sizes >60			
	n_1	s_1	$f(0)_2$	$g(0)_1$	n_2	s_2	$f(0)_2$	$g(0)_2$	n_3	s_3	$f(0)_3$	$g(0)_3$
Pacific white-sided dolphin, *Lagenorhynchus obliquidens*	3	4.34	0.874	0.561	5	26.36	0.516	1.000	3	70.30	0.292	1.000
Risso's dolphin, *Grampus griseus*	4	5.32	0.874	0.561	6	21.94	0.516	1.000	0	—	—	—
Bottlenose dolphin, *Tursiops truncatus*	3	2.32	0.874	0.561	5	7.31	0.516	1.000	0	—	—	—
Common dolphins, *Delphinus* spp.	13	9.56	0.874	0.561	21	34.69	0.516	1.000	31	196.09	0.292	1.000
Striped dolphin, *Stenella coeruleoalba*	0	—	—	—	0	—	—	—	2	34.66	0.292	1.000
Northern right whale dolphin, *Lissodelphis borealis*	5	10.57	0.874	0.561	2	9.79	0.516	1.000	2	75.67	0.292	1.000
Killer whale, *Orcinus orca*	2	2.40	0.874	0.561	0	—	—	—	0	—	—	—

Large cetaceans (Truncated at 5.55 km; sea states 0–5)

	n_1	s_1	$f(0)_1$	$g(0)_1$
Sperm whale, *Physeter macrocephalus*	2	2.32	0.701	0.902
Humpback whale, *Megaptera novaeangliae*	10	3.47	0.701	0.902
Blue whale, *B. musculus*	29	2.07	0.701	0.902
Fin whale, *B. physalus*	14	2.20	0.701	0.902

Total area size: 264,270 km^2
Total length of transect line surveyed: 3,357 km in Beaufort sea states 0–5; 1,262 km in Beaufort sea states 0–2.

Figure 3. Distribution of perpendicular sighting distances (thick lines) and Hazard model fits (thin lines) for species and group-size strata used in analysis of 1991 ship survey data.

of two populations (Barr 1969), but they must be applied with caution. Lo (1994) performed simulations to evaluate statistical power and realized α-errors (Type I errors) for three commonly used confidence-interval tests under the assumptions of normal, log-normal, gamma, and Poisson distributions. For the two tested methods that were based on the extent of overlap of the confidence intervals for the population means, Lo's simulations revealed that power and realized α-levels varied considerably and unsystematically between distributions. In contrast, the third method, which was based on the confidence interval of the difference (d) between population means, was shown to provide consistent results across all four types of distributions, as well as a realized α-level equal to the intended value (in this case, $\alpha = 0.05$).

For the comparison of seasonal differences in cetacean abundance, we have adapted Lo's (1994) third approach, shown to be robust for a variety of dis-

tributions, for use with bootstrap confidence intervals rather than the theoretical confidence intervals used by Lo (1994). Given the summer and winter abundance estimates, N_s and N_w, respectively, the difference, d, was calculated as $N_s - N_w$. A confidence interval for the difference, CI(d), was determined by first calculating the differences, d^*, between the 1,000-bootstrap abundance estimates for summer and winter (N_s^* and N_w^*, respectively) which were generated in the individual analyses described above. Bootstrap 95% confidence intervals were then calculated from this set of 1,000 d^* values using the BC_a method described by Efron and Tibshirani (1993). (This method is superior to the simpler percentile method of determining bootstrap confidence intervals, because it allows for bias correction and acceleration. In this case bias is the deviation of the mean bootstrap value of d^* from the actual difference, d, and acceleration is the rate of change in the standard error of d with respect to the true difference.) The true seasonal abundance estimates were determined to be significantly different at $\alpha = 0.05$ if the 95% confidence interval of their difference did not contain zero. Approximate probability levels for each comparison were determined by iteratively constructing a range of confidence intervals and identifying the threshold α-levels (to three significant figures) at which the confidence intervals just included zero.

An analogous approach was used to test for differences in the distribution of individual species between the summer and winter survey periods. Only species with a minimum of eight sightings in each season were included in the geographic analysis. Geographic strata representing north/south and inshore/offshore regions were created on the basis of physical features of the study area. The north/south boundary was set at Pt. Arguello to differentiate the largely north-south oriented coastline of central and northern California from the topographically complex Southern California Bight region. This also coincides with the previously defined boundary between Areas 2 and 3 (Fig. 1) used to estimate abundances for the aerial surveys. An inshore/offshore boundary was chosen along the approximate 2,000-m isobath to provide similar survey effort in shallower nearshore regions and in deeper offshore waters.

Because of sample size limitations, analyses were performed separately for the two pairwise geographic stratifications (north/south and inshore/offshore). For each region, geographically stratified abundance estimates and bootstrap distributions of the estimates were obtained, and the proportion, q, of the abundance estimate that was in the inshore or south stratum, respectively, was calculated for each season. The difference in this proportion, d_q, between seasons was then used as the basis of the bootstrap confidence-interval test. For each of the 1,000 pairs of geographically stratified bootstrap abundance estimates, the proportion, q^*, of the overall abundance attributable to the south or inshore stratum, respectively, was calculated for both seasons, and the difference, d_q^*, was determined. This bootstrap distribution of the 1,000 differences between the summer and winter proportions was then used to construct BC_a confidence intervals for d_q. If the 95% confidence interval for d_q did not contain zero, then the distribution was considered to be significantly different

between the two seasons. Approximate probability levels were determined iteratively as described above for the abundance test.

RESULTS

Species Seen

Thirteen identified cetacean species were sighted on both the shipboard and aerial surveys (Table 3). Short-beaked and long-beaked common dolphins (*Delphinus delphis* and *Delphinus capensis*) were also seen on both surveys, but they could not be reliably distinguished on the aerial surveys, and comparisons therefore will be limited to the entire genus. Additionally, beaked whales of the genus *Mesoplodon* were sighted during both surveys; however, because of the difficulty in differentiating species in this genus and the large number of sightings of unidentified beaked whales from both platforms, no comparisons will be presented for this genus or for Cuvier's beaked whale (*Ziphius cavirostris*). Gray whales (*Eschrichtius robustus*), short-finned pilot whales (*Globicephala macrorhynchus*), and a northern right whale (*Eubalaena glacialis*) were observed only during the winter surveys. Striped dolphins (*Stenella coeruleoalba*) and Baird's beaked whales (*Berardius bairdii*) were seen only during the summer survey.

1991–1992 Seasonal Comparison

Several species that were seen were excluded from the seasonal comparison for a variety of reasons (Table 3). Harbor porpoises (*Phocoena phocoena*) were excluded because the survey design was not appropriate for this coastal species (Fig. 4), and therefore the seasonal estimates are considered too imprecise for a meaningful comparison. Beaked whales and minke whales (*Balaenoptera acutorostrata*) were excluded because insufficient sightings were made to estimate the detection function for this "small whale" group. Gray whales are known to migrate through California waters during winter and feed in arctic waters during summer; consistent with this migration, no sightings were made during summer and therefore no tests were performed. The remaining excluded species were also seen only in one season, and insufficient sightings were made to perform a meaningful comparison.

Among the eleven species that were included in the analysis, the observed patterns of abundance were variable (Table 3). No significant seasonal differences in abundance were identified for five cetacean species: offshore bottlenose dolphins (*Tursiops truncatus*), Dall's porpoises (*Phocoenoides dalli*), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and humpback whales (*Megaptera novaeangliae*). All of the remaining delphinid species were substantially more abundant during winter than during summer, despite the expected downward bias in the winter abundance estimates (see Discussion). This included the cool-temperate species, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and northern right whale dolphins (*Lissodelphis borealis*), as well as

Table 3. Species seen, abundance estimates and results of significance tests for differences in abundance between summer (1991) ship surveys and winter (1991 and 1992) aerial surveys off the California coast. See text for a discussion of caveats, biases, and conclusions regarding seasonal patterns. Key: n = number of sightings, N = abundance estimate, CV = coefficient of variation for abundance estimate, d = observed difference in abundance estimates. $CI(d)$ is BC_a bootstrap confidence interval for d, and P = probability value for observed difference, obtained using iterative BC_a bootstrap confidence interval estimation process. Where number of sightings is given in parentheses, only off effort' sightings were made.

Species	Summer 1991 ship survey			Winter 1991 & 1992 aerial surveys[a]			d (N_s-N_w)	Bootstrap test results		
								CI (d)		P
	n_s	N_s	CV_s	n_w	N_w	CV_w		L95%	U95%	value
Species included in the analysis:										
Dall's porpoise	50	34,737	0.295	38	26,111[b]	0.296	8,616	-8,528	41,376	0.221
Pacific white-sided dolphin	11	5,899	0.453	21	121,693	0.466	-115,794	-257,513	-33,042	<0.001*
Risso's dolphin	10	3,980	0.574	19	32,376	0.456	-28,396	-68,590	-6,292	0.004*
Bottlenose dolphin	8	1,169	0.640	8	3,260	0.487	-2,091	-6,259	865	0.176
Common dolphins	65	92,202	0.246	27	305,694	0.340	-213,492	-469,675	-33,042	0.012*
Northern right whale dolphin	9	5,377	0.656	31	21,332	0.428	-15,955	-41,201	-1,493	0.036*
Killer whale	2	294	0.987	2	51	0.689	243	-77	1,175	0.246
Sperm whale	2	142	0.818	3	2,679[b]	0.990	-2,537	-9,831	208	0.297
Blue whale	29	1,838	0.523	1	30	0.990	1,808	508	4,821	<0.001*
Fin whale	14	943	0.790	2	49	0.745	894	3	3,448	0.048*
Humpback whale	10	1,062	0.576	8	319	0.407	743	-30	2,458	0.064
Additional species seen during the surveys:										
Harbor porpoise	31	—	—	18	—	—	—	—	—	—
Striped dolphin	2	796	0.701	0	—	—	—	—	—	—
Short-finned pilot whale	0	—	—	(1)	—	—	—	—	—	—
Baird's beaked whale	(2)	—	—	0	—	—	—	—	—	—
Cuvier's beaked whale	7	—	—	3	—	—	—	—	—	—
Mesoplodont beaked whales	1	—	—	2	—	—	—	—	—	—
Northern right whale	0	—	—	1	—	—	—	—	—	—
Gray whale	0	—	—	25	2,844	0.347[c]	—	—	—	—
Minke whale	4	—	—	3	—	—	—	—	—	—

[a] These values are the same as those in Forney *et al.* (1995), except for killer whales and fin whales, for which two minor errors were identified and corrected, and for species to which footnote b applies.

[b] Estimated correction factors for availability bias were included in the abundance calculations for these species (see text).

[c] This estimate captures only animals migrating through California at the time of the surveys. See Buckland *et al.* (1993b) for an overall population estimate.
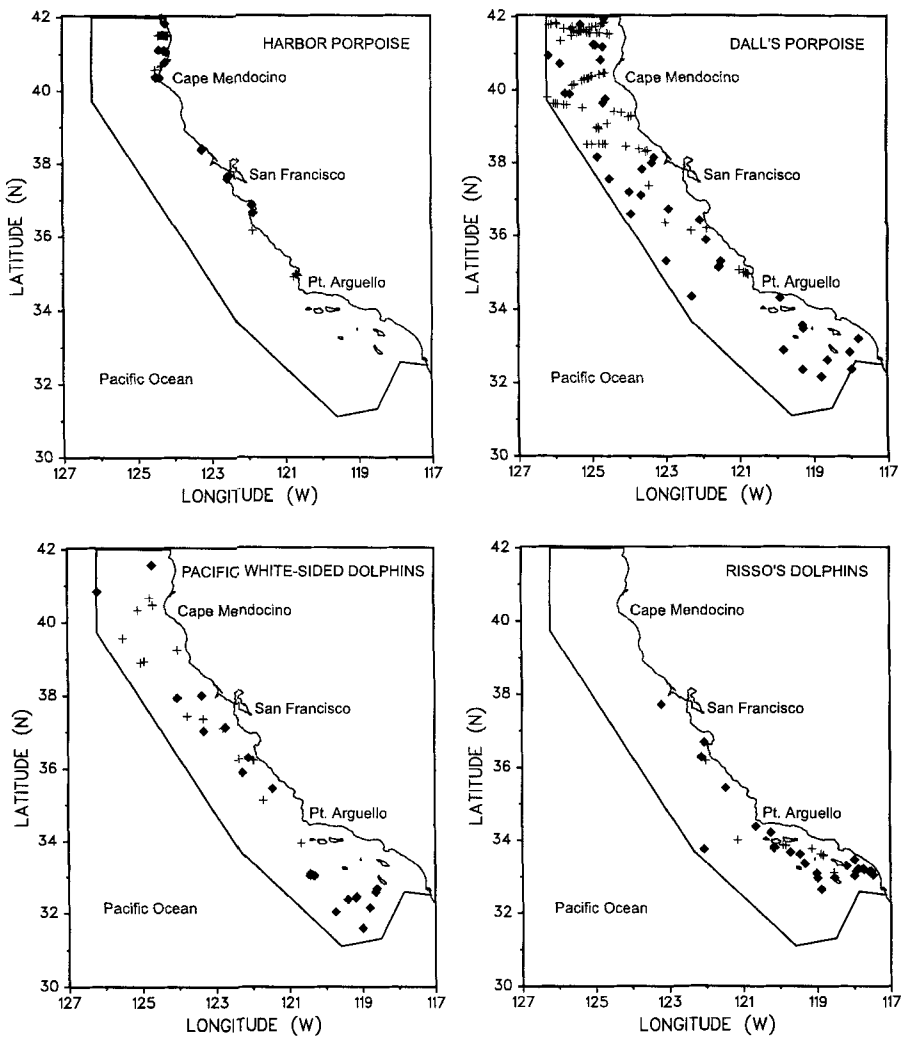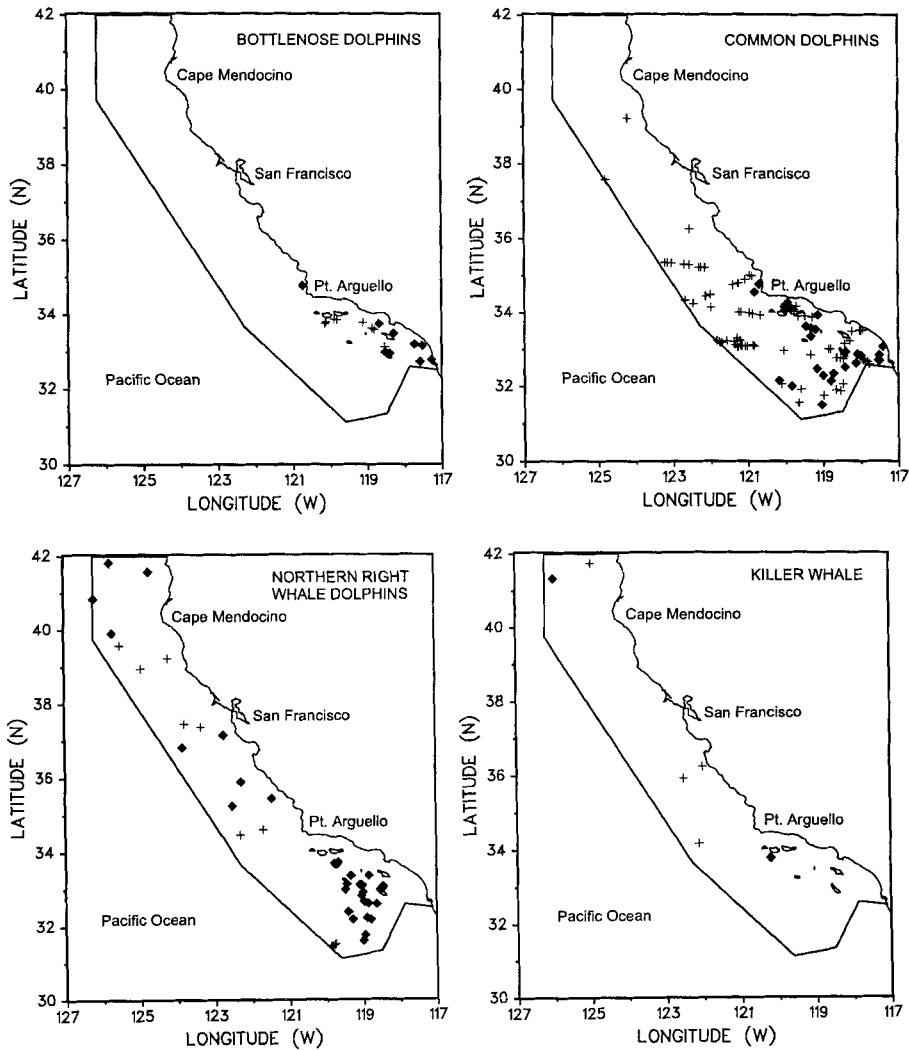
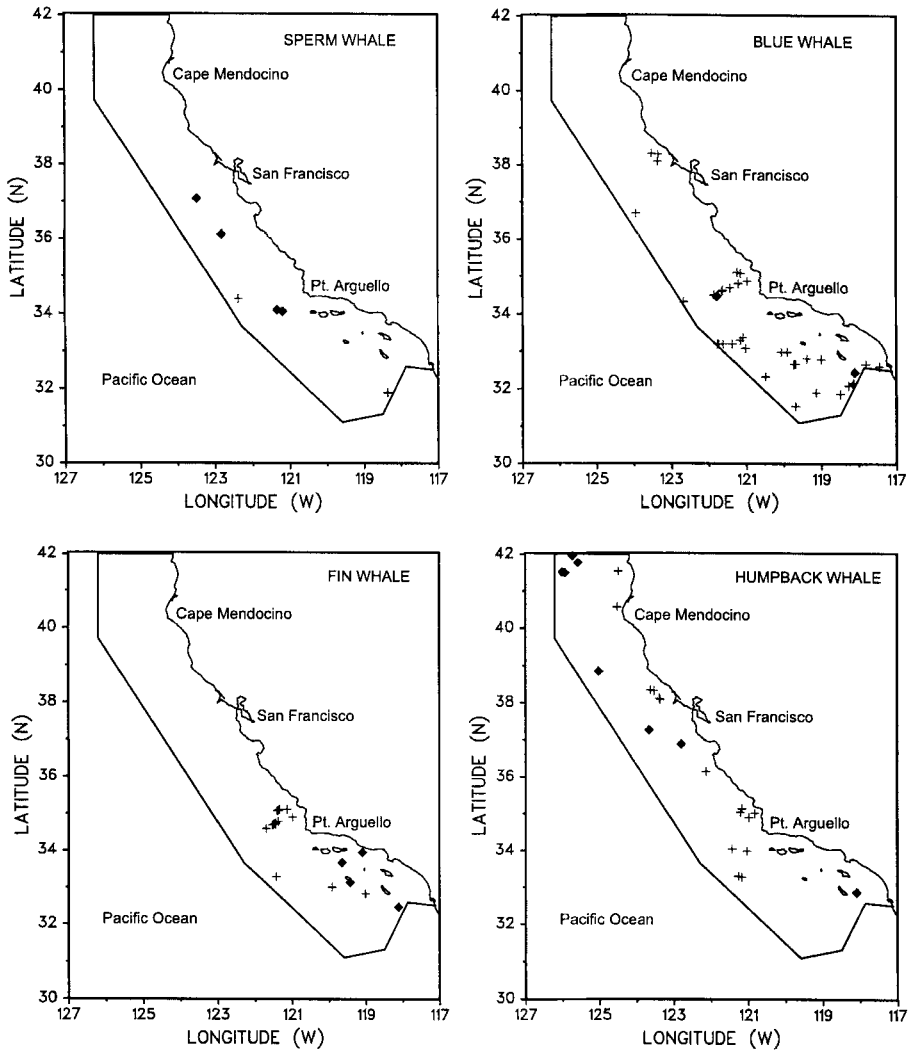* Indicates statistical significance.

Figure 4. Sighting locations for individual species within California study area, based on winter 1991 and 1992 aerial surveys (◆) and summer 1991 shipboard surveys (+).

the more warm-temperate to tropical common dolphins (*Delphinus* spp.) and Risso's dolphins (*Grampus griseus*).

With the exception of Risso's dolphin, all of these delphinids also exhibited significant differences in distribution between seasons (Table 4). A significantly greater proportion of northern right whale dolphins was found inshore of the 2,000-m isobath during winter than in summer, representing a winter influx of this species into the continental shelf region of the Southern California Bight (Fig. 5). Common dolphins exhibited significant differences in distribution indicating offshore and northward movement out of the Southern Cal-

Table 4. Seasonal differences in the distribution of species with at least eight sightings in each season. Statistical probabilities are given based on the bootstrap confidence-interval test for equality of proportion inshore or south in summer and winter.

Species	Total abundance		Proportion inshore of 2,000-m isobath			Proportion south of Pt. Arguello		
	Summer	Winter	Summer	Winter	P value	Summer	Winter	P value
Dall's porpoise	34,737	26,111	0.51	0.50	0.994	0.00	0.27	<0.001*
Pacific white-sided dolphin	5,899	121,693	0.81	0.87	0.606	0.00	0.18	<0.001*
Risso's dolphin	3,980	32,376	0.90	0.98	0.603	0.87	0.31	0.062
Bottlenose dolphin	1,169	3,260	1.00	1.00	—	1.00	0.97	0.674
Common dolphins	92,202	305,694	0.59	0.98	<0.001*	0.80	0.98	0.031*
Northern right whale dolphin	5,377	21,332	0.09	0.83	<0.001*	0.47	0.72	0.287
Humpback whale	1,062	319	0.85	0.18	0.024*	0.18	0.05	0.708

* Indicates statistical significance.

Figure 5. Sighting locations for individual species within California study area, based on winter 1991 and 1992 aerial surveys (♦) and summer 1991 shipboard surveys (+).

ifornia Bight during summer (Fig. 5). Pacific white-sided dolphins were rare off Southern California in the summer but were commonly found there during winter (Fig. 4). A similar, statistically significant, winter influx of animals into Southern California waters was observed for Dall's porpoises (Fig. 4).

As expected, based on known migration patterns, blue whales were significantly more abundant in summer, when they are known to feed off the California coast. Surprisingly, however, seasonal abundances for humpback whales, which undertake similar migrations, were not significantly different. This is particularly interesting when considered along with the results of the inshore/

Figure 6. Sighting locations for individual species within California study area, based on winter 1991 and 1992 aerial surveys (♦) and summer 1991 shipboard surveys (+).

offshore distribution test, which indicates that a significantly greater proportion of the population was found farther offshore during winter than during summer (Table 4, Fig. 6). Although fin whales (*Balaenoptera physalus*) were seen in both seasons, they were significantly more abundant during the summer survey.

No significance tests could be performed on the distribution of school sizes for the two seasons due to small sample sizes, but mean school sizes were greater during winter than summer for Pacific white-sided dolphins (152 *vs.* 32), common dolphins (515 *vs.* 107) and Risso's dolphins (48 *vs.* 15), whereas

northern right whale dolphins exhibited similar mean school sizes (19 *vs.* 25) during winter and summer, respectively.

Variances for the abundance estimates are high for both surveys (CVs range between 0.25 and 0.99, Table 3), in particular for species which had few sightings. For most species, the variance in the number of sightings, *n*, contributed the most to the overall variance in abundance. The exception to this occurred with species that were seen frequently and exhibited a wide range of school sizes, such as common dolphins, Pacific white-sided dolphins, and northern right whale dolphins. The variance of *f*(0) generally contributed less than these other two components. These patterns were consistent between the winter aerial and summer shipboard surveys.

DISCUSSION

Using this simple bootstrap test, significant differences in the abundance of six cetacean species were identified (Table 3), and five species exhibited significant seasonal changes in distribution. However, it is important to interpret the differences in the context of biases inherent in the different methodologies used for the two surveys. The most important difference between aerial and shipboard surveys is the magnitude of availability bias (Marsh and Sinclair 1989), which is the proportion of animals missed because they are submerged during the time the survey platform passes through the area. From a ship traveling at 10 kn (18 km/hr), the likelihood of missing diving animals is much smaller than from an aircraft traveling at 100 kn (185 km/hr), despite the ability to see into the water from aircraft. Thus, for most species the abundance estimates obtained from the aerial surveys will be underestimates. The exceptions to this would be species such as common dolphins that occur in large schools in which some individuals are generally at or near the surface at all times. In theory, correction factors for this bias should be applied to aerial survey abundance estimates for all species, but in practice, they are not available for most. In many of the cases below, the aerial survey abundance estimate is larger than the shipboard estimate despite the expected downward bias, and therefore the comparison is still meaningful. In these cases the seasonal differences represent minimum values, and the true differences will depend upon the diving behavior and differential detectability of each species. Because the nature and extent of expected biases vary, the results and identifiable patterns will be discussed separately for each species. The discussion is arranged taxonomically according to the classification of Perrin (1989).

Dall's porpoise—On ship surveys, attraction of Dall's porpoises to the survey vessel (to ride the bow wave) can cause an upwards bias in abundance estimates (Turnock and Quinn 1991). For the 1991 ship survey used in this analysis, Barlow (1995) concluded that vessel attraction was not a problem, based on an examination of behaviors exhibited by Dall's porpoises at the time of sighting and on the proportion of all groups that approached the vessel.

Aerial survey abundance estimates for Dall's porpoises are expected to be biased downwards, because Dall's porpoises occur in small groups and are

easily missed if they are submerged at the moment the aircraft passes overhead. No correction factor for this availability bias is currently available for Dall's porpoise, and without such a correction, a direct comparison of shipboard and aerial survey abundance estimates is not possible. On the basis of taxonomic relationship and general similarities in diving behavior, body size and school size, one might expect the proportion of Dall's porpoises missed to be similar to the proportion of harbor porpoises missed. For this reason, in this analysis, the correction factor 0.324 (CV = 0.174) obtained for the harbor porpoise (Calambokidis *et al.* 1993*a*) was included in the abundance calculations for Dall's porpoises to calculate an approximate corrected estimate of abundance. During the bootstrap procedure, variance in the correction factor was included by randomly drawing a value from a normal distribution with mean 0.324 and standard deviation 0.056. Thus, $g(0)$ for this species includes corrections for both perception and availability biases during the aerial survey.

The resulting winter abundance estimate of 26,111 Dall's porpoises (CV = 0.296) is similar to the summer shipboard estimate of 34,737 animals (CV = 0.295), and the difference is not statistically significant (P = 0.221). This suggests that there was no pronounced seasonal change in abundance within the study area between winter 1991 and 1992 and summer 1991. However, a significantly greater proportion of the population was found south of Pt. Arguello during winter (Table 4, Fig. 4). Previous studies have also documented higher sighting rates off central and northern California in fall and off southern California in winter (Morejohn 1979; Dohl *et al.* 1980, 1983). Seasonal shifts in the regions of high density were found in those studies, but the patterns were variable from year to year. This previously observed interannual variability is consistent with the results of a 1993 survey (Mangels and Gerrodette 1994, Barlow and Gerrodette 1996), which showed a dramatically lower abundance of Dall's porpoises during 1993 (a warmer year) in comparison to 1991 (a cooler year). Because California represents the approximate southern extent of this species' range in the eastern North Pacific, this probably reflects variable southward movement into California from waters off Oregon and Washington. Overall, the evidence indicates that Dall's porpoises shift their distribution southward during cooler-water periods on both interannual and seasonal time scales.

Pacific white-sided dolphin—This species exhibited the most dramatic difference between summer and winter abundance estimates within the California study area in 1991–1992, with the winter estimate being over 20 times higher (121,693 *vs.* 5,899; Table 3). This difference was determined to be highly significant by the bootstrap test (P < 0.001) and may, in fact, be even more pronounced than indicated in this analysis, because a higher proportion of animals is expected to be missed from aircraft. The large difference in abundance estimates suggests seasonal movement out of the California study area, either offshore or northward into waters off Oregon and Washington. The complete ship survey, extending 300 nmi offshore, resulted in only one sighting of Pacific white-sided dolphins in waters beyond the present study area boundary (Barlow 1995), indicating that the population probably moved

northward in summer, rather than offshore. A statistically significant (Table 4) seasonal north-south shift within California is evident by the virtual absence of animals off southern California in summer 1991, despite their frequent occurrence there in winter 1991 and 1992 (Fig. 4).

Green *et al.* (1992, 1993) hypothesized a seasonal movement of Pacific white-sided dolphins between California and Oregon/Washington based on aerial surveys conducted between April 1989 and September 1990 in these two northern states. They found high densities of Pacific white-sided dolphins in late spring and early summer, with lower densities observed during the winter. However, if the summer 1991 California abundance (5,899) and the peak abundance in Oregon and Washington (38,512, obtained in 1989 and 1990) are combined, the overall estimate is still considerably smaller than the 1991 and 1992 winter California estimate (121,693). This could indicate that animals move beyond Oregon and Washington into other regions farther north or offshore, or it could be considered as evidence for interannual variability in the extent of seasonal movement into waters off Oregon and Washington. If there is marked interannual variability, then abundances obtained in different regions in different years would not be additive.

Risso's dolphin—The abundance of Risso's dolphins within the California study area was almost an order of magnitude higher in winter (32,376; CV = 0.456) than in summer (3,980; CV = 0.574), and the bootstrap test was highly significant ($P = 0.004$). The true difference in abundance is likely to be even more pronounced than indicated by these estimates, because the higher value is expected to be biased downwards due to the greater availability bias during aerial surveys. Although Risso's dolphins are conspicuous when seen from the air, groups often dive synchronously and therefore can easily be missed during aerial surveys.

Despite the significant difference in seasonal abundance, there was no significant difference in distribution within the study area for the two survey periods (Table 4, Fig. 4). In both seasons they were seen most frequently in the Southern California Bight and were also observed off central California. Green *et al.* (1992) suggested seasonal movement of Risso's dolphins from California into Oregon and Washington waters in spring and summer. This is consistent with the observed decrease in abundance between the winter and summer survey periods in this study. The surveys conducted in Oregon and Washington in 1989, 1990, and 1992 also indicated pronounced interannual differences in the degree of seasonal change (Green *et al.* 1992, 1993). Sighting plots for the complete 1991 ship survey extending 300 nmi (556 km) offshore (Barlow 1995) indicate that Risso's dolphins were also common in offshore waters of northern California, west of the present study area. It is not known to what extent they may inhabit these offshore waters during winter and spring. Barlow's (1995) total abundance estimate for the larger California study area, 8,496 animals (CV = 0.415), is only about one-quarter of the winter estimate, suggesting that many Risso's dolphins were outside the California study area at the time of the summer/fall 1991 survey. The degree of movement into Mexican waters is unknown, but a large gap in the distribution of

Risso's dolphin sightings between about 29°N latitude and the tip of Baja California, Mexico (approximately 22°N) (Leatherwood *et al.* 1980, Mangels and Gerrodette 1994) suggests that animals off the U.S. west coast and northern Baja California may be distinct from Risso's dolphins found farther south in tropical waters of the Gulf of California and the eastern tropical Pacific.

Offshore bottlenose dolphin—Along the California coast there apparently are two populations of bottlenose dolphins: an offshore population and a coastal population that is found within about 1 km or less from shore (Hansen 1990, Hanson and Defran 1993). On both of the surveys in this study, the bottlenose dolphins seen were considered to belong to the offshore population (Forney *et al.* 1995, Barlow 1995), and the discussion presented here will be limited to these offshore animals.

During both the winter and summer surveys, offshore bottlenose dolphins were uncommon throughout the study area and were seen primarily off southern California (Fig. 5). Abundance estimates were higher during winter (3,260; $CV = 0.487$) than in summer (1,169; $CV = 0.640$), but this difference was not significant ($P = 0.176$; Table 3). Availability bias for this species is expected to be higher on aerial surveys than on shipboard surveys, so the true seasonal difference may be greater than indicated in this analysis, perhaps even significant. As with Risso's dolphins, additional sightings of bottlenose dolphins were made farther offshore off northern California during the complete summer survey (Barlow 1995), but it is unknown to what extent they may inhabit these waters year-round. Barlow's overall abundance estimate of 1,503 bottlenose dolphins ($CV = 0.481$) is slightly closer to the winter estimate. Bottlenose dolphins are also known to occur off Baja California, Mexico (Mangels and Gerrodette 1994, Wade and Gerrodette 1993), but no information on movements between Mexican and U.S. waters is presently available.

Common dolphins—Common dolphins off California were recently recognized to include two species, short-beaked and long-beaked common dolphins (Heyning and Perrin 1994). Differences in color pattern enabled the two species to be distinguished during the 1991 shipboard surveys, but it was not possible to differentiate them reliably from the air during the 1991–1992 winter surveys. For this analysis, the two species of common dolphins therefore have been combined to produce one overall abundance estimate. The vast majority (96%) of common dolphins identified during the ship survey were short-beaked common dolphins (Barlow 1995), and therefore this species is expected to be the main contributor to the patterns of abundance and distribution described below.

Availability bias during aerial surveys is expected to be relatively small for common dolphins, which often occur in large groups numbering in the hundreds and in which at least some animals are generally at the surface. Although smaller groups were also observed, these sightings did not contribute much to the total abundance estimate. Thus, the aerial survey estimate of 305,694 common dolphins ($CV = 0.340$) is likely to have only a small downward bias. Depending on the magnitude of this bias, the true difference in abundance between the summer shipboard survey (92,202; $CV = 0.246$) and the winter

aerial survey (305,694; CV = 0.340) may be greater than suggested in this analysis.

The large and statistically significant difference ($P < 0.012$; Table 3) in the abundance of common dolphins during summer 1991 and winter 1991–1992 is a surprising contrast to patterns observed off Southern California during the late 1970s (Dohl et al. 1986). In that earlier study, common dolphins were much less abundant and showed seasonal patterns directly opposite to the current findings (15,448, CV = 0.36 in winter-spring and 57,270, CV = 0.17 in summer-fall, with a September maximum approaching 100,000 animals; Dohl et al. 1986). Overall, common dolphin abundance off California has increased dramatically since the late 1970s (Barlow 1995, Forney et al. 1995). Anganuzzi and Buckland (1994) present evidence of a concomitant decrease in short-beaked common dolphin abundance in the eastern tropical Pacific between about 1979 and 1992, suggesting a large-scale shift in the distribution of this species in the eastern North Pacific. Interestingly, however, the northern limit of common dolphins was similar in the summers of 1979/80 (Smith et al. 1986) and 1991 (Barlow 1995) at about 40°N.

In contrast to this well-defined long-term increase in abundance, the patterns of seasonal abundance and distribution appear to be more complex than can be resolved with the available data. Barlow's ship-survey estimate for all common dolphins within the region extending 300 nmi (556 km) offshore of California (245,579 animals; CV = 0.260) is similar to the winter estimate, but it is unknown whether the common dolphins seen offshore on that survey may be there year-round (resulting in an even greater winter abundance for this larger study area), or whether they represent a summer influx of animals into offshore regions. During the recent surveys, common dolphins were not found north of about Pt. Arguello during winter 1991 and 1992 but were common well north of there during summer 1991 (Fig. 5), especially in offshore regions (Barlow 1995). Both the north/south and the inshore/offshore components of this movement were determined to be significant in these analyses (Table 4). During the late 1970s, common dolphins were much less abundant in the northern part of the Southern California Bight during winter (Dohl et al. 1986), and only one sighting was made north of Pt. Arguello during monthly surveys off central and northern California in 1980–1983 (Dohl et al. 1983). This contrasts with sightings reported as far north as 40°N during the summers of 1979 and 1980 (Smith et al. 1986). Thus the northward extent of common dolphin distribution appears to vary interannually and with changing oceanographic conditions.

Northern right whale dolphin—Northern right whale dolphins are observed in a wide range of group sizes, including small, inconspicuous, synchronously diving groups for which availability bias is likely to be high during aerial surveys, and large, active schools which have at least some members visible at all times. The majority of sightings made during the winter aerial surveys were of the former type and, therefore, the overall abundance estimate is probably biased downward by an unknown, but possibly large, amount. Both the shipboard and aerial surveys were probably affected by perception bias, because

the low surfacing profile of northern right whale dolphins makes them difficult to detect from a ship, and their dark coloration can make them hard to see from the air when light conditions are not optimal. An estimated correction factor for perception bias ($g(0)$ in Tables 1 and 2) was included in the analyses for both surveys, but availability bias of unknown magnitude remains for the winter aerial survey estimate.

Despite the expected downward bias for the winter aerial survey estimate, a statistically significant ($P = 0.037$) difference in abundance was identified between winter 1991 and 1992 (21,332; CV = 0.428) and summer 1991 (5,377; CV = 0.656). The distribution of sightings, which is not expected to be affected by perception or availability bias, also differs significantly for these two surveys (Fig. 5, Table 4). In winter northern right whale dolphins were widespread throughout the continental shelf region of the Southern California Bight, but no sightings were made there in summer. During both seasons they were commonly observed off central and northern California, and in summer they were also observed off Southern California near the offshore edge of the present study area (Barlow 1995). This evidence for a winter influx of northern right whale dolphins into shelf waters of the Southern California Bight in 1991–1992 is consistent with similar findings made during the late 1970s (Leatherwood and Walker 1979, Dohl et al. 1980). During the summer, some of these animals may be farther offshore, as suggested by the distribution of sightings and the total abundance estimate of 9,342 (CV = 0.567) for the 1991 summer ship survey extending out 300 nmi (556 km) (Barlow 1995). However, this abundance is only about half of the winter estimate, suggesting that further northward and/or offshore movement may occur during the summer.

Killer whale—The estimates of abundance for killer whales in summer (294; CV = 0.987) and winter (51; CV = 0.689) have large variances and are not statistically distinguishable ($P = 0.246$). During the aerial surveys animals may have been missed due to availability bias, as these animals occur in relatively small groups that often dive synchronously. Thus, the winter estimate is probably biased downward, bringing the two estimates closer together. The number of sightings for both surveys is very small (2 sightings each), and although these results cannot be considered conclusive, they are consistent with past studies indicating that this species is infrequently observed off California, without any apparent centers of concentration or seasonal patterns (Dohl et al. 1980, 1983). Green et al. (1992) also observed killer whales year-round off Oregon and Washington.

The nature of movements of killer whales in this region is poorly understood. Three individuals that were photographed in Monterey Bay have also been photographed in Glacier Bay, Alaska (Goley and Straley 1994), indicating that at least some killer whales found off California undertake long-range movements. A recent systematic photoidentification study comparing killer whales sighted off California with those in other regions has provided further evidence of long-range movements and points to the existence of several distinct killer whale types in this region (Black et al. 1997).

Sperm whale—Many studies have documented long dive times for sperm whales, ranging up to 138 min in some cases (Watkins *et al.* 1985) and more commonly being on the order of 15–90 min, followed by 4–10 min at the surface (Leatherwood *et al.* 1982*b*). Males tend to dive for longer periods than females with calves. During ship surveys, availability bias is expected to be relatively small, because the conspicuous blow patterns of sperm whales allow them to be seen from great distances, and therefore the time window for sighting the animals is relatively long (Barlow and Sexton 1996). During aerial surveys availability bias is expected to be high, resulting in an abundance estimate that may be low by a factor of three to eight (Barlow 1994). A conservative minimum correction was therefore included in this analysis by multiplying the aerial survey abundance estimate and corresponding bootstrap abundance estimates by a factor of three. Using this minimum correction, the winter abundance estimate for sperm whales in this study (2,679; CV = 0.990) is not significantly greater ($P < 0.296$) than that for the summer ship survey within the same study area (142; CV = 0.818). However, the ability to resolve seasonal differences is low because both abundance estimates are based on very few sightings (Fig. 6) and variances are high.

Seasonal movements of sperm whales have been documented for the North Pacific (Gosho *et al.* 1984), but detailed regional data are scarce. Based on monthly aerial surveys in 1980–1983 off central and northern California, Dohl *et al.* (1983) reported sightings of sperm whales in all months except July, with a large degree of interannual variability during the three-year study period. Monthly surveys conducted in 1975–1978 off southern California yielded only one sighting in this region (Dohl *et al.* 1980). In contrast, recent year-round surveys in a small area offshore of southern California in 1993–1994 resulted in 11 sightings of sperm whales during January–March and October–November (Carretta *et al.* 1995), suggesting a possible seasonal pattern of occurrence in that region.

Blue whale—The abundance estimates for blue whales presented in this study are in close agreement with documented seasonal movements of this species. Blue whales feed off the California coast from roughly June through November, and move southward to waters off Mexico in winter and spring (Calambokidis *et al.* 1990). The summer abundance estimate in the present study is 1,838 (CV = 0.523), only slightly less than the abundance of 2,250 blue whales (CV = 0.381) estimated to be in the larger study area used by Barlow (1995). The winter abundance estimate of 30 blue whales (CV = 0.990) is based on only a single sighting made in March 1992, and has a large degree of uncertainty. The difference in seasonal abundance estimates is highly significant ($P < 0.001$), reflecting the seasonal presence of feeding aggregations of blue whales off California during the summer months.

Fin whale—The movement patterns of fin whales in the eastern North Pacific are not well understood, but previous studies have documented the year-round presence of fin whales off California, with an increase in abundance during summer and fall (Dohl *et al.* 1980, 1983; Carretta *et al.* 1995; Barlow 1994). The results of this study are consistent with these past findings, with

the summer estimate (943 animals, CV = 0.790) being significantly higher (P = 0.048, Table 3) than the winter estimate (49 animals, CV = 0.745). Both abundance estimates have high variances, and a correction factor for the aerial survey estimate, if available, would bring the two values closer together. Although these uncertainties make it difficult to evaluate abundance patterns for this species, it is possible that the seasonal difference in fin whale abundance off California is less pronounced than previously thought. Overall, the available data point to a year-round presence of fin whales off southern California with an apparent summer increase in abundance. Although sample sizes were too small to include this species in the distribution tests, there also appears to be a change in distribution to include waters off central and northern California during summer (Fig. 6). It is not known where the additional animals may be at other times of the year, but whaling records indicate that some fin whales marked off southern California in winter were later taken between central California and the Gulf of Alaska (Mizroch et al. 1984), suggesting long-range movements of this species.

Humpback whale—California represents one of several major summer feeding areas for North Pacific humpback whales, which have recently been divided into four discrete migratory populations based on photoidentification and genetic studies (Baker et al. 1990, 1993; Barlow 1994; Calambokidis et al. 1996). The population which breeds off coastal Mexico and Costa Rica in winter and spring (Steiger et al. 1991, Calambokidis et al. 1993b) is known to feed off California, Oregon, and Washington, and to a lesser extent British Columbia, during the summer and fall. At first glance the pattern of seasonal abundances in this study (Table 3) reflects this migration, with a higher estimate during summer (1,062; CV = 0.576) than winter (319; CV = 0.407). However, this difference is not significant (P = 0.064), and there are two important caveats. The summer estimate is less precise than the smaller estimate of 626 (CV = 0.411) obtained by Barlow (1995) in his complete analysis of all data out to 300 nmi (556 km), because it is based on a smaller sample size for estimation of the detection function of large whales (55 sightings in this study versus 113 sightings available to Barlow). The estimate of 626 is also more consistent with the independent mark-recapture estimate of 597 (CV = 0.07) based on photoidentification studies (Calambokidis and Steiger 1994). The winter estimate is likely to be biased downwards due to availability bias of an unknown magnitude, because humpback whales generally are seen alone or in small groups that may dive synchronously for several minutes at a time (Leatherwood et al. 1982b) and therefore can easily be missed during aerial surveys. When these two caveats are taken into account, the abundance estimates are much more similar, in seeming contradiction to the well-documented seasonal movements of this population.

Feeding humpback whales begin to appear off California in spring, and it is possible that the winter abundance estimate included some early migrants for the 1991 and 1992 seasons. Calambokidis et al. (1996) report that six of ten humpback whales photographed (presumably nearshore off California) in March and April were seen again later in the season off California, indicating

that at least some humpback whales from the California feeding population appear early in the season. But many of the winter aerial survey sightings were made about 80–100 nmi (148–185 km) from the coast, which contrasts with the more coastal distribution of humpback whales during the summer (Fig. 6; Calambokidis 1993*b*, Barlow 1995). The inshore/offshore difference was determined to be statistically significant (Table 4) in the present analysis. It is thus possible that these winter animals are merely traveling through the offshore region of California en route to other feeding areas to the north. At the present time, however, it remains unclear whether the humpback whales seen in offshore waters of California in early spring are part of the California feeding population, or whether they are part of a different population whose summer feeding destination is unknown, such as the one found off the Revillagigedos Islands in winter (Barlow 1994).

Conclusions

The diversity of seasonal patterns of abundance and distribution revealed for the 11 species discussed above during the 1991–1992 study period is testimony to the dynamic and diverse nature of the California Current. Many of the observed patterns reflect the mixing of temperate and tropical waters in this region, with seasonal variation in the distribution of each type of water mass. Where sufficient information is available, the distribution and abundance of many California cetaceans appear to vary with oceanographic changes on both seasonal and interannual time scales, reflecting large-scale movement of individuals in these populations. Seasonal patterns observed in future years may well differ from those observed in 1991–1992.

Further studies of the relationships between oceanographic conditions, prey availability, and the distribution and abundance of individual cetacean species are needed to improve our understanding of the ecology of these marine predators. Research incorporating information on the habitats in which individual California cetacean species are found is also likely to improve our quantitative estimates of abundance. Comprehensive shipboard surveys covering more of the individual species' range (at a minimum, the waters off California, Oregon, and Washington) during different seasons are likely to provide the most effective means of resolving and understanding the observed patterns of distribution and abundance. Ideally, cooperative research with Mexico would be possible to study those species extending southward into Mexican waters.

Finally, the bootstrap confidence-interval test employed in this comparison may prove useful in similar situations where standard statistical techniques are not valid because various assumptions are not met. The simplicity of the method and its requirement for only a bootstrap distribution of the parameter of interest make it a versatile technique for comparing two estimates when error distributions cannot be assumed to be normal. The main limitation of this method is that the underlying bootstrap procedures and confidence-interval calculations can be computationally intensive, depending on the size and nature of the data set.

ACKNOWLEDGMENTS

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